CHROMOSOMAL RACES IN EASTERN NORTH AMERICAN SPECIES OF HEDYOTIS (HOUSTONIA)[1]

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In a phylogenetic study of the North American species of *Hedyotis* (including *Houstonia*) (Rubiaceae), Lewis (1962 b) reported diploid and tetraploid races in populations of *H. caerulea, H. polypremoides* (Gray) Shinners, and *H. purpurea.* Reference was made to a more extensive study of the occurrence of infraspecific polyploidy. The purpose of this paper is to report these findings.

Chromosome numbers of 116 collections of species in the *H. caerulea* and *H. purpurea* groups were determined. P. M. C. meiosis or somewhat less frequently mitosis was studied in immature flower buds fixed in the field. The methods used to prepare slides were identical to those described for *Hedyotis* (Lewis, 1962b). In addition, representative permanent slides were mounted in euparal. Voucher specimens for each collection are filed in the herbaria of the U. S. National Museum (US), the Southern Methodist University (SMU), or Indiana University (IND; one collection).

The nomenclature of the *H. purpurea* complex follows the revision by Terrell (1959) except that the taxa are treated under *Hedyotis* rather than *Houstonia* (Lewis, 1961). This does not imply acceptance of *Hedyotis* by Terrell.

RESULTS

The chromosome numbers of *Hedyotis purpurea, H. longifolia, H. canadensis, H. nuttalliana* (= *Houstonia tenuifolia* Nutt.), *H. caerulea*, and *H. michauxii* (= *Houstonia serpyllifolia* Michx.), are listed with voucher data and, in parentheses, the number of plants examined. Although the chromosome numbers of several collections were published by Lewis (1962b), as indicated by an asterisk, they are included for completeness and as a basis for mapping.

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1. *H. purpurea* (L.) T. & G.

1a. *H. purpurea* var. *purpurea*

n = 6. SOUTH CAROLINA: Edgefield Co., 4 miles WSW of Owdoms, *Terrell & Barclay 3430* (3). TEXAS: Newton Co., 2.8 miles S of Newton, *Lewis 5620* (5)*.

n = 6, n = 12. TENNESSEE: Polk Co., 0.5 mile N of Hwys. 64 & 30 junction, *Lewis 5638* (4 2*n*, 2 4*n*).

n = 12. GEORGIA: Gilmer Co., 3.9 miles NE of Ellijay, *Lewis 5645* (3). MARYLAND: Montgomery Co., Wheaton, *Terrell 3525* (4). NORTH CAROLINA: Guilford Co., Guilford College, *Terrell 3244* (1)*: Jackson Co., summit of Whitesides Mountain, *Terrell & Barclay 3472* (3); Macon Co., SE of Highlands, *Terrell & Barclay 3463* (2); Standing Indian Wildlife Management Area, *Terrell & Barclay 3478* (2). TENNESSEE: Cheatham Co., near Kingston Springs, *Terrell & Barclay 3360;* Cumberland Co., 1.5 miles W of Ozone, *Terrell & Barclay 3516* (3); Polk Co., 2.5 miles E of Hwys. 64 & 30 junction, *Lewis 5643* (atypical) (4); Sullivan Co., near Sullivan-Carter Co. line & Hwy. 19E, *Terrell & Barclay 3524* (3). VIRGINIA: Sussex Co., along Nottoway River W of Homeville, *Terrell 3636* (2).

1b. *H. purpurea* var. *calycosa* (Gray) Fosberg

n = 6. TENNESSEE: Wilson Co., Cedars of Lebanon State Park, *Terrell & Barclay 3339* (5); W border of Lebanon, *Terrell & Barclay 3340* (6).

n = 12. ALABAMA: Franklin Co., 7 miles E of Russellville, *Terrell & Barclay 3499* (3); just E of Russellville, *Terrell & Barclay 3361* (2); Jackson Co., 3 miles W of Scottsboro, *Terrell & Barclay 3485* (3). MISSISSIPPI: Carroll Co., 1.5 miles E of Carrolton, *Lewis 5634* (atypical) (3). TENNESSEE: Maury Co., 16 miles NW of Lewisburg, *Terrell & Barclay 3351* (4)*; Meigs Co., 7 miles S of Decatur, *Terrell & De Selm 3246* (1).

1c. *H. purpurea* var. *montana* (Small) Fosberg

n = 6. TENNESSEE-NORTH CAROLINA: Carter Co.-Mitchell Co., summit of Roan Mountain, *Terrell & Barclay 3615* (2).

2. *H. longifolia* (Gaertn.) Hook.

2a. *H. longifolia* var. *longifolia*

n = 6. MASSACHUSETTS: Middlesex Co., Horn Pond, Woburn, *E & B Terrell 3595* (3).

n = 6, n = 12. MINNESOTA: Chisago Co., St. Croix River at Taylors Falls, *Likhite*, July 1961 (2 2*n*, 5 4*n*).

n = 12. ONTARIO: Norfolk Co., Turkey Point, *C & M Heimburger*, 15 July 1961 (1).

2b. *H. longifolia* var. *compacta* (Terrell) Lewis

n = 6. GEORGIA: Meriwether Co., 5 miles W of Greenville, *Terrell & Barclay 3410* (2). NORTH CAROLINA: Alexander Co., base of Rocky Face Mountain, *Terrell 3257* (1)*. SOUTH CAROLINA: Abbeville Co., E side of Savannah River, *Terrell & Barclay 3424* (atypical) (1); Anderson Co., ca. 11 miles NNE of Anderson, *Terrell & Barclay*

3451 (2); Lexington Co., ca. 10 miles S of Columbia, *Terrell & Barclay 3444* (atypical) (3). VIRGINIA: Augusta Co., 11 miles NE of Hwys. 42 & 250 junction, *E & B Terrell 3569* (3); Frederick Co., 2 miles WNW of Gore, *E & B Terrell 3539* (2); Page Co.-Madison Co. line, Milepost 47, Skyline Drive, Shenandoah Natl. Pk., *E & B Terrell 3577* (3); Rappahannock Co., Hazel Mountain Overlook, Shenandoah Natl. Pk., *Terrell 60-11* (2) (no voucher); Shenandoah Co., 4.5 miles SW of Jerome, *E & B Terrell 3567* (3). Another collection is quite atypical: GEORGIA: Dade Co., Lookout Mountain, *Terrell & De Selm 3254* (1).

n = 12. MARYLAND: Frederick Co., Boonesboro Mountain Rd. & Hwy. 40 junction, *E & B Terrell 3533* (4). SOUTH CAROLINA: Edgefield Co., near Hwy. 378 & 67 junction, *Terrell & Barclay 3429* (3). VIRGINIA: Augusta Co.-Albemarle Co., 0.4 miles S of Milepost 97, Skyline Drive, Shenandoah Natl. Pk., *E & B Terrell* 3570 (3); Bedford Co., Milepost 90, Blue Ridge Parkway, *Terrell 3250* (2); Rockingham Co.-Greene Co., Sandy Bottom Overlook, Skyline Drive, Shenandoah Natl. Pk., *E & B Terrell 3573* (2). WEST VIRGINIA: Pendleton Co., 5 miles N of Hwy. 33 & Spruce Knob rd. junction, *E & B Terrell 3545* (3).

2c. *H. longifolia* var. *glabra* (Terrell) Lewis

n = 6. NORTH CAROLINA: Jackson Co., summit of Whitesides Mountain (type locality), *Terrell & Barclay 3473* (3); Macon Co., near Highlands, *Terrell 3255* (1)*; Slick Rock, SE of Highlands, *Terrell & Barclay 3464* (2).

3. *H. canadensis* (Willd. ex R. & S.) Fosberg

n = 6. TENNESSEE: Cheatham Co., near Kingston Springs, *Terrell & Barclay 3358* (4).

n = 12. INDIANA: Clark Co., 4 miles NW of Henryville, *Terrell 3251* (1)*. TENNESSEE: Marion Co., below Hales Bar Dam, *Terrell & Barclay 3480* (3). ONTARIO: Bruce Co., Bruce Peninsula, Red Bay, *Heimburger & Price*, 17 June 1961 (2).

4. *H. nuttalliana* Fosberg

n = 6. ALABAMA: Randolph Co., ca. 5 miles W of Wedowee, *Terrell & Barclay 3397* (4); Saint Clair Co., 0.5 mile W of Hwys. 35 & 53 junction, *Terrell & Barclay 3391* (3). ARKANSAS: Montgomery Co., 11.5 miles WSW of Norman, *Lewis 5169* (2)*. GEORGIA: Heard Co., 3 miles SW of Franklin, *Terrell & Barclay 3401* (5). NORTH CAROLINA: Stokes Co., Hanging Rock State Park, *Terrell 3243* (1)*. OKLAHOMA: Leflore Co., Lake Wister State Park, *Lewis 5161* (2)*. SOUTH CAROLINA: Lexington Co., ca. 4 miles E of Lexington Co.-Saluda Co. line, *Terrell & Barclay 3445* (3). VIRGINIA: Shenandoah Co., 2.6 miles E of Liberty Furnace, *E & B Terrell 3560* (3).

5. *H. caerulea* (L.) Hook.

5a. *H. caerulea* var. *caerulea*

n = 8. ALABAMA: Blount Co., ca. 3 miles E of Cullman, *Terrell*

& Barclay 3387 (3); Randolph Co., ca. 5 miles W of Wedowee, *Terrell & Barclay 3398* (3); Saint Clair Co., 0.5 mile W of Hwys. 35 & 53 junction, *Terrell & Barclay 3392* (3); Talladega Co., 2-3 miles W of Talladega Co.-Clay Co. line & Hwy. 77, *Terrell & Barclay 3396* (2). ARKANSAS: Clark Co., 2.4 miles SE of Alpine, *Lewis 5171* (3)*; Dallas Co., 1.9 miles S of Ouachita, *Lewis 5172* (3)*; Hot Spring Co., 1.5 miles NE of Donaldson, *Lewis 5613* (1). GEORGIA: Gilmer Co., 3.9 miles NE of Ellijay, *Lewis 5646* (1). INDIANA: Brown Co., near Trevlac, *Heiser & Ellis 4763* (IND) (3). KENTUCKY: Logan Co., 1.3 miles SW of Auburn, *Lewis 5602* (2); Metcalf Co., 3.1 miles E of Wisdom, *Lewis 5605* (4). NORTH CAROLINA: Alleghany Co., 2 miles NE of Blue Ridge Parkway & Hwy. 21 junction, *Terrell 3242* (2); Jackson Co., ca. 4 miles E of Cashiers, *Terrell & Barclay 3455* (3); Macon Co., Nantahala River & Hwy. 64, *Terrell & Barclay 3479* (3). SOUTH CAROLINA: Lexington Co., ca. 4 miles E of Lexington Co.-Saluda Co. line, *Terrell & Barclay 3446* (3). TENNESSEE: Cheatham Co., near Kingston Springs, *Terrell & Barclay 3359* (3); Stewart Co., 12.9 miles WSW of Dover, *Lewis 5601* (2); Kentucky Lake & Hwy. 79, *Lewis 5610* (2).

n = 9. ARKANSAS: Hot Spring Co., 3.6 miles NNE of Hwys. 67 & 210 junction, *Lewis 5612* (2).

n = 16. CONNECTICUT: Litchfield Co., 1-1/2 miles S of junction 112 & 7, Salisbury Twp., *Terrell 3662* (1); Tolland Co., 3 miles S of Rockville, *Terrell 3663* (2); near State Line Pond, *Terrell 3664* (3). MAINE: York Co., North Berwick, *E & B Terrell 3591* (1). MARYLAND: Frederick Co., Catoctin Creek & Hwy. 17, *E & B Terrell 3538* (1); Montgomery Co., Wheaton Regional Park, *Terrell 3526* (2). MASSACHUSETTS: Franklin Co., 3 miles S of Northfield, *Terrell 3667* (3); Worcester Co., 1/2 mile N of Hardwick, *Terrell 3665* (3). NEW HAMPSHIRE: Cheshire Co., 3 miles E of Winchester, *Terrell 3666* (1); Coos Co., lower slopes of Mount Washington (alt. 2500 ft.), *E & B Terrell 3589* (2); Grafton Co., Hanover, *Fosberg 39838* (2). NORTH CAROLINA: Guilford Co., Guilford College, *Terrell 3231* (5)*; Stokes Co., NW of Francisco, *Terrell 3239* (1)*. PENNSYLVANIA: Franklin Co., 0.5 mile N of Richmond Furnace, *Terrell 3629* (2); Juniata Co., 5 miles NE of East Waterford, *Terrell 3628* (4); Perry Co., 1 mile SE of Shermandale, *Terrell 3627* (3). SOUTH CAROLINA: Edgefield Co., ca. 4 miles WSW of Owdoms, *Terrell & Barclay 3431* (2). TENNESSEE: Cumberland Co., 7 miles SE of Mayland, *Terrell & Barclay 3514* (3); Knox Co., Knoxville, *De Selm*, 1 May 1962 (1). VERMONT: Windham Co., 2 miles W of Brattleboro, *Terrell 3668* (2). VIRGINIA: Hanover Co., 2 miles NW of Doswell, *Terrell 3631* (2); Page Co.-Madison Co., Big Meadows, Shenandoah Natl. Pk., *E & B Terrell 3575* (2). WEST VIRGINIA: Tucker Co., 8 miles S of Davis, *E & B Terrell 3544* (2); 1-2 miles N of Thomas, *E & B Terrell 3540* (1). ONTARIO: Toronto (introduced), *Heimburger*, 5 May 1961 (4) (omitted from map in Fig. 2).

n = 24. VIRGINIA: Sussex Co., along Nottoway River W of Homeville, *Terrell 3634* (1).

5b. *H. caerulea* var. *faxonorum* (Pease & Moore) Fosberg

n = **16.** NEW HAMPSHIRE: Coos Co., below summit of Mount Washington (alt. 6000 ft.), *E & B Terrell 3586* (4).

6. *H. michauxii* Fosberg

n = **16.** NORTH CAROLINA: Macon Co., Standing Indian Wildlife Area, *Terrell & Barclay 3477* (3); Transylvania Co., 0.5 mile N of Davidson River & Hwy 64 junction, *Terrell & Barclay 3460* (4). TENNESSEE: Monroe Co., Cherokee National Forest, *De Selm*, 1 May 1962 (3). TENNESSEE-NORTH CAROLINA: Carter Co.-Mitchell Co., summit of Roan Mountain, *Terrell & Barclay 3520* (5).

n = **24.** NORTH CAROLINA: Alleghany Co., 2 miles NE of Blue Ridge Parkway & Hwy. 21 junction, *Terrell 3241* (1)*.

7. Putative hybrids or intergrading collections

7a. *H. longifolia—H. purpurea*

n = **6.** SOUTH CAROLINA: McCormick Co., 2.5 miles NW of Mount Carmel, *Terrell & Barclay 3425* (1) (< longifolia).

n = **12.** GEORGIA: Elbert Co., 2 miles W of Hwys. 72 & 79 junction, *Terrell & Barclay 3423* (2) (< longifolia); Rabun Co., ca. 7 miles S of North Carolina-Georgia line & Hwy. 28, *Terrell 3147* (1); Walton Co., 4 miles NE of Monroe, *Terrell & Barclay* 3420 (2) (< longifolia). TENNESSEE: Cumberland Co., 2 miles NW of Mayland, *Terrell & Barclay 3513* (3) (< purpurea).

7b. *H. canadensis > — H. purpurea*

n = **12.** INDIANA: Clark Co., 4 miles NW of Henryville, *Terrell 3252* (1).

7c. *H. caerulea—H. michauxii*

n = **16.** WEST VIRGINIA: Tucker Co., just above Blackwater Falls, *E & B Terrell 3542* (5).

DISCUSSION

The basic chromosome number of *Hedyotis purpurea*, *H. longifolia*, *H. canadensis*, and *H. nuttalliana* is $x = 6$. The basic chromosome number of *H. caerulea* and *H. michauxii* is $x = 8$. These data agree with the morphological evidence: the first four species are closely related and were included by Terrell (1959) in the *H. purpurea* group; the last two species are so alike that herbarium material sometimes is difficult to distinguish.

A dash, —, is used here to indicate morphological intergradation. The second author prefers to use this symbol instead of ×, as in this case additional knowledge about the species is needed to attribute their intermediacy to hybridization. He believes that botanists should restrict the use of × to instances in which evidence of hybridization has been thoroughly studied. The symbols > and < were used by others (cf. Li, 1957; Hardin, 1958). For example, *H. canadensis > — H. purpurea* denotes specimens which intergrade but are more similar to the former species.

In *H. purpurea* (Fig. 1) our sampling indicates that tetraploid populations are in the great majority. The only known $2n$ populations are in the southern part of the range. One population included both $2n$ and $4n$ individuals. The sampling is not sufficient to show any geographic separation of chromosomal races, if such exists. Var. *montana*, the only known stations for which are on Roan Mountain and Grandfather Mountain, is diploid at the former station (not shown in Fig. 1).

In contrast to *H. purpurea*, *H. longifolia* has almost twice as many $2n$ populations as $4n$. These are found in the north

Figure 1. Generalized range (enclosed by dashed line) of H. *purpurea* and locations of diploid and tetraploid collections. Var. *montana* not shown. New England distribution of var. *calycosa* not shown.

as well as in the south, and one population in Minnesota contains individuals with both chromosome numbers. Var. *glabra,* restricted to the southern Appalachians, is diploid on the basis of three collections.

Plants of *H. canadensis* from only four localities were studied but these included samples from the extremes of the species range in Tennessee and Ontario. On the basis of the small sample, the tetraploids prevail over the diploids in a proportion similar to that for *H. purpurea.* With both $2n$ and $4n$ races in Tennessee, no geographic separation of the forms is apparent. Only $2n$ individuals were found among plants of *H. nuttalliana* from 8 stations in 7 states, from Virginia to Oklahoma. This sample is sufficiently large and widespread to indicate that tetraploid individuals must be rare in *H. nuttalliana* if they exist. Infraspecific polyploidy is probably unimportant in the recent evolution of the species. On the basis of the frequency of diploidy and tetraploidy, with the high frequency of tetraploidy representing the higher stage of evolution, the species in the $x = 6$ group can be ranked from the simplest to the most specialized as: *H. nuttalliana* ($2n$ only), *H. longifolia* ($2n{:}4n = 2{:}1$), *H. purpurea* and *H. canadensis* ($2n{:}4n = 1{:}3$). Using this criterion, *H. nuttalliana* is the least evolved species of the series, a position corroborating the results of Lewis (1962b) based chiefly on morphological evidence.

Among 45 collections of *H. caerulea* var. *caerulea* sampled from a wide area of the species range, 18 were diploid ($n = 8$), 25 were tetraploid ($n = 16$), one was aneuploid ($n = 9$), and one was hexaploid ($n = 24$). Thus, this species consists predominantly of $2n$ and $4n$ populations, with the latter slightly outnumbering the former in our sample. The base number is $x = 8$. The chromosomal races appear to have partly distinct distributions: the diploid race is widely distributed in the southern United States (Fig. 2) and in our sample occurs only south of the glacial boundary. Only tetraploids are known in New England, but they do occur also in certain parts of the South. The single collection of var. *faxonorum,* a variety restricted primarily to higher altitudes in the White Mountains, was tetraploid.

On the basis of a single population of *H. michauxii,* Lewis

(1962b) reported the species as hexaploid. Additional sampling has shown, however, that $4n$ and $6n$ races exist, the former occurring much more frequently. The species is limited in distribution to the higher regions of the southern and central Appalachians, a distribution interestingly associated with the finding of two polyploid races and no diploid forms in a subgenus where "pure" polyploid species are infrequent.

In the P. M. C.'s of all plants examined, bivalent formation and separation by and large were regular. Occasionally 1 to 3 quadrivalents were observed at metaphase I in the $4n$ plants (e.g., *H. purpurea, Terrell & Barclay 3351; H. caeru-*

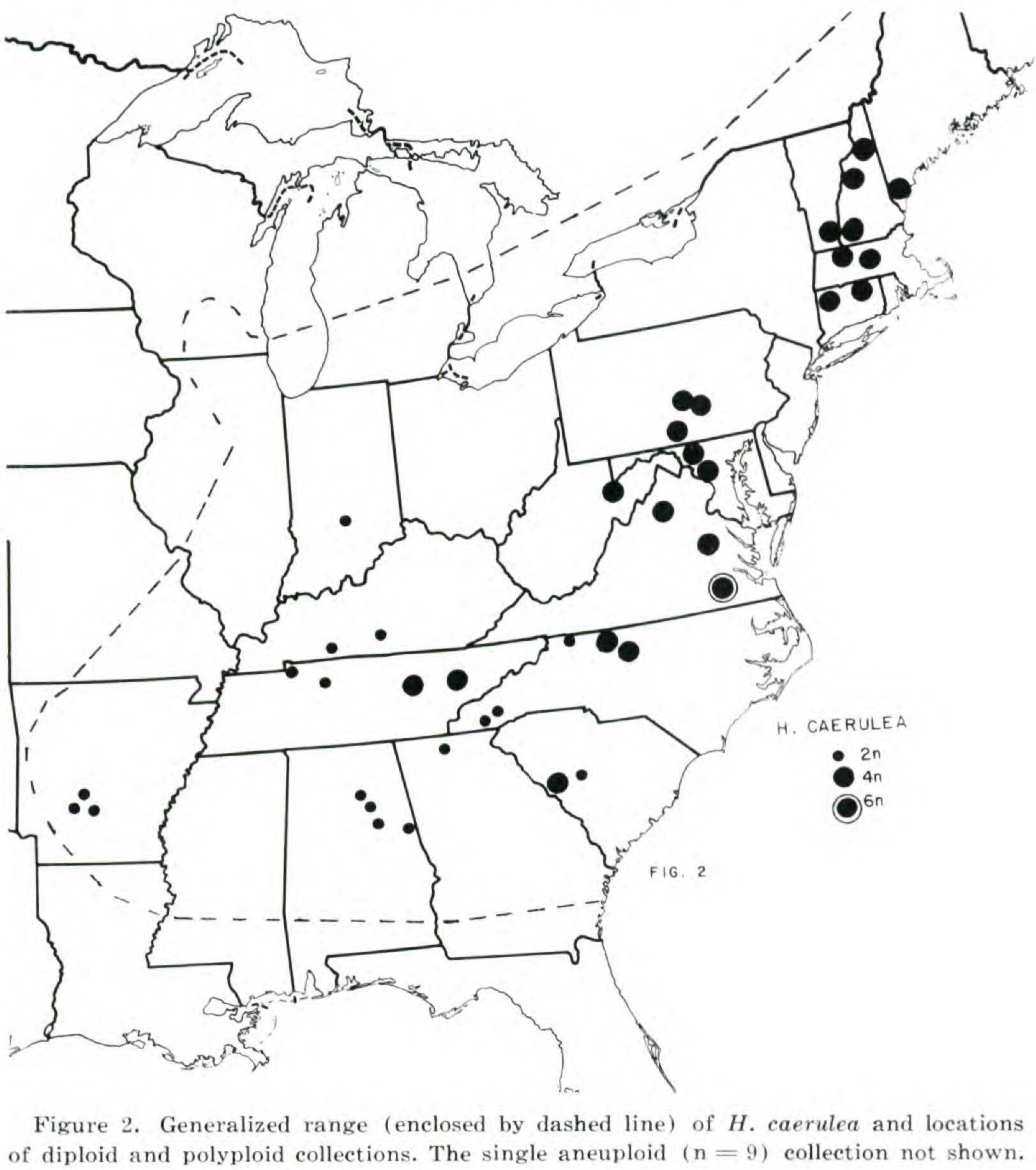

Figure 2. Generalized range (enclosed by dashed line) of *H. caerulea* and locations of diploid and polyploid collections. The single aneuploid ($n = 9$) collection not shown.

lea, Terrell 3627), but these were exceptional. Spindle disturbances were not observed. In one cell, a plant of *H. caerulea (Lewis 5610)* had $2n = 15$, but all other mitotic cells had $2n = 16$ and in the P. M. C.'s $n = 8$. Although statistical data are not available, plump, well-stained pollen grains were noted for most diploids and tetraploids. If the fertility of the tetraploids was decreased markedly in comparison with the diploids it was not apparent from observations of pollen.

Seven collections were of intermediate or intergrading morphology. Certain of these are putative hybrids. As no definite evidence of hybridization is available, we are using a dash (—) to connect the two names. This is intended to indicate intergradation without necessarily suggesting hybridization as its cause. In the seven collections diploid and tetraploid populations were found, with the latter more frequent. Of the five collections of *H. purpurea* — *H. longifolia*, a diploid *(Terrell & Barclay 3425)* had regular pairing at metaphase I as did all P. M. C.'s examined from the tetraploid individuals of *T. & B. 3420* and *3513*. Only mitosis was observed in the other two collections of *H. longifolia* — *H. purpurea* and in *H. canadensis* — *H. purpurea*. Meiosis in *H. caerulea* — *H. michauxii* was regular; this population is not thought to be of hybrid origin. Pollen was more or less normal in individuals of the seven collections. In general, the chromosome data indicate that chromosome number *per se* is no barrier to hybridization in these species within each ploidy level, i.e. $x = 6$ and $x = 8$. The chromosome numbers in the *H. purpurea* group are entirely compatible with the data from morphology expressed in the taxonomic treatment of this group by Terrell (1959) but the few admittedly preliminary chromosome counts listed in the same paper should be ignored.

As more cyto-population research is completed, it becomes apparent that varying chromosome numbers for a species are much more common than hitherto suspected. In the Rubiaceae alone, where very few cytological studies have been completed, infraspecific polyploidy has been recorded for species of 13 genera, particularly in the Rubieae (Fagerlind, 1937; Ehrendorfer, 1961), *Coffea* and *Coprosma* (cf.

Darlington & Wylie, 1956), *Bouvardia* (Lewis, 1962a), and *Hedyotis* subg. Oldenlandia (Lewis, 1959, 1962b).

In *Hedyotis* subg. Edrisia, in which the species under discussion are classified, chromosome numbers of 25 species are known (Lewis, 1962b). Of these, seventeen species are diploid, four species are diploid and tetraploid, one species is diploid, tetraploid, and hexaploid, two species are tetraploid, and one species is tetraploid and hexaploid. Twenty-three species are euploid and two have recorded aneuploid individuals. Thus six species or 24% of the North American species studied have infraspecific polyploidy, 4% exhibit infraspecific aneuploidy, and 4% exhibit both infraspecific polyploidy and aneuploidy. All of these species are heterostylous perennials and with one exception are herbaceous. No chromosomal plasticity is known among the eight annual species of the subgenus or among the species having only short-styled flowers. This suggests a certain correlation in the subgenus between the heterostylous species constructed for outbreeding and the perennial habit with the occurrence of infraspecific polyploidy and aneuploidy.

The distributions of the diploid and tetraploid races of *H. caerulea*, *H. purpurea*, and *H. longifolia* may be grouped into two categories, viz., those with different geographic distributions and those without such tendencies. As an example of the first kind, the $2n$ race of *H. caerulea* occupies a southern range while the $4n$ race has a more northern distribution. Possibly the tetraploid race colonized areas drastically altered by glaciation in the northern region of the species' present range, while the ancestral race remained predominantly south of the glacial boundary (cf. Stebbins, 1950). It also appears that the $4n$ race is now successfully competing with the $2n$ race somewhat south of the southern limits of the last glaciation. The high altitude distribution and the polyploid races of *H. michauxii* also suggest the colonization of less favorable environments by a polyploid species. That this tendency is not universal, even for species in the same subgenus, is suggested by the infraspecific distributions for *H. purpurea* and *H. longifolia*. Their diploid and tetraploid races are about equally distributed and do not appear to have either peripheral or central concentrations although we did not sample their entire ranges.

When herbarium specimens from all of these collections were compared, tetraploid and diploid (and hexaploid) plants of each taxon looked just alike; there were no observable gross morphological differences in plants of different ploidy levels and it is clear that these are autopolyploids. Five out of the six species had polyploid populations. Autopolyploidy is an essential feature of the evolution of the *H. caerulea* and *H. purpurea* groups.

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